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NON-RANDOM VESSEL DISTRIBUTION IN WOODS: PATTERNS, MODES, DIVERSITY, CORRELATIONS

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ABSTRACT

Vessel grouping is a form of non-random distribution that becomes functionally valuable when the background consists of non-conductive imperforate tracheary elements (fiber-tracheids and libriform fibers); ungrouped vessels, randomly placed, often occur in an all-tracheid background. Types of vessel grouping are described and illustrated: diagonal, tangential, radial, median radial bands, and growth rings. Other non-random distributions considered include degrees and kinds of cable construction, patchy vessel distributions, vessel displacement related to succulence, and patterns involving successive cambia. Non-random vessel distributions inevitably involve non-random placement of imperforate tracheary elements, so that a parallel set of mechanical adaptations is often simultaneously achieved. Correlations between various types of non-random vessel patterns and possible physiological factors are hypothesized. Most correlations involve enhanced conductive safety, but vessel distribution related to water and photosynthate storage, resistance to torsion, and increased longevity of xylem are cited. Non-randomness of vessels is a source of diversity in wood structure that can be achieved readily (as growth rings show) and polyphyletically. These modifications offer numerous ways in which wood histology can be repatterned for probable adaptations in conductive physiology, mechanical strength, and storage capability, perhaps by means of regulatory genes. Grouping of vessels into vascular bundles in primary xylem of stems and leaves in dicots is a form of non-randomness, and the significance of vascular bundles (as opposed to steles) as adaptive forms of organization is considered briefly. Monocots differ from dicots in rarely having division of labor in tracheary elements within an organ, but monocots exhibit tradeoffs in which conductive efficiency (vessel presence in an organ) and conductive safety (tracheids but no vessels in an organ) can be achieved within a single plant.

Key words: cable construction, conductive pathways, lianas, mechanical strength, tracheary elements, vascular bundles, vines, wood anatomy, wood evolution, xylem.

INTRODUCTION

Some of the most conspicuous features of wood anatomy have received little or no comment despite their inherent interest. The tendency of vessels to group or not to group as seen in wood transections, evident in the figures of Grew (1682), was only recently the topic of an explanatory hypothesis (Carlquist 1984). Similarly, one can note in Grew's figures a phenomenon related to vessel grouping, but with additional implications. Grew's figures of rosaceous woods (apple, pear, plum) show randomness of vessel distribution, but others (oak, see Fig. 1 here), show that vessels are absent from some areas of axial secondary xylem, and are confined to diagonal bands. Grew's (1682) figure of wood of "a vine" (almost certainly *Vitis vinifera* L.) corresponds to Fig. 14 here. The paired rows of large vessels, none of which touch rays, are accurately if simply figured by Grew.

Conceding that non-randomness in vessel distribution in dicot woods has been depicted for a long time, how can one define it? What kinds of non-random distributions are there? What correlations between these distributions and other features of the plant (ecology, habit, physiology) can be found? An earlier exploration of non-randomness in vessels in wood of Papaveraceae (Carlquist and Zona 1988a) resulted in description of a distinctive phenomenon, termed "vessel restriction patterns" there. Additional instances were reported by Carlquist (1988a). Although that descriptive term is still valid, it is only one of a number of non-random vessel distribution types. The term "non-random" is therefore used

here as a more inclusive way of describing vessel positioning in woods.

We often think of vessels are randomly placed throughout a dicot wood, but in fact, that condition obtains only in a minority of species. The evolutionary value of randomness is presumably that the vessels as a primary conductive system are equidistant from each other. Potentially, this would offer water supply across shorter bridges. Woods with random vessel placement are also usually woods in which tracheids occur, and in which vessels are solitary (Carlquist 1984). A tracheid background provides a subsidiary conductive system that can maintain water columns should vessels, which are much more prone to embolizing than tracheids (Ewers 1985; Hargrave et al. 1995), fill with air. Air in an embolized tracheid spreads into an adjacent tracheid rarely, whereas air spreads easily from one vessel element to another (Zimmermann 1971). Randomness or near-randomness of vessel placement results in greater dispersion of vessel pathways and therefore potentially greater conductive safety but does not correlate with a particular ecology. Tracheid-bearing species with randomly placed vessels and scalariform perforation plates may characterize perpetually moist cloud forests (Actinidiaceae, Chloranthaceae, Illiciaceae), but species with simple perforation plates in randomly placed vessels, combined with tracheid presence, can be found in dry or desert localities (e.g., Krameriaceae, Rosaceae: Carlquist and Hoekman 1985).

There are probably numerous evolutionary strategies of wood construction in which non-random vessel placement represents an adaptive expression. The polyphyletic nature of

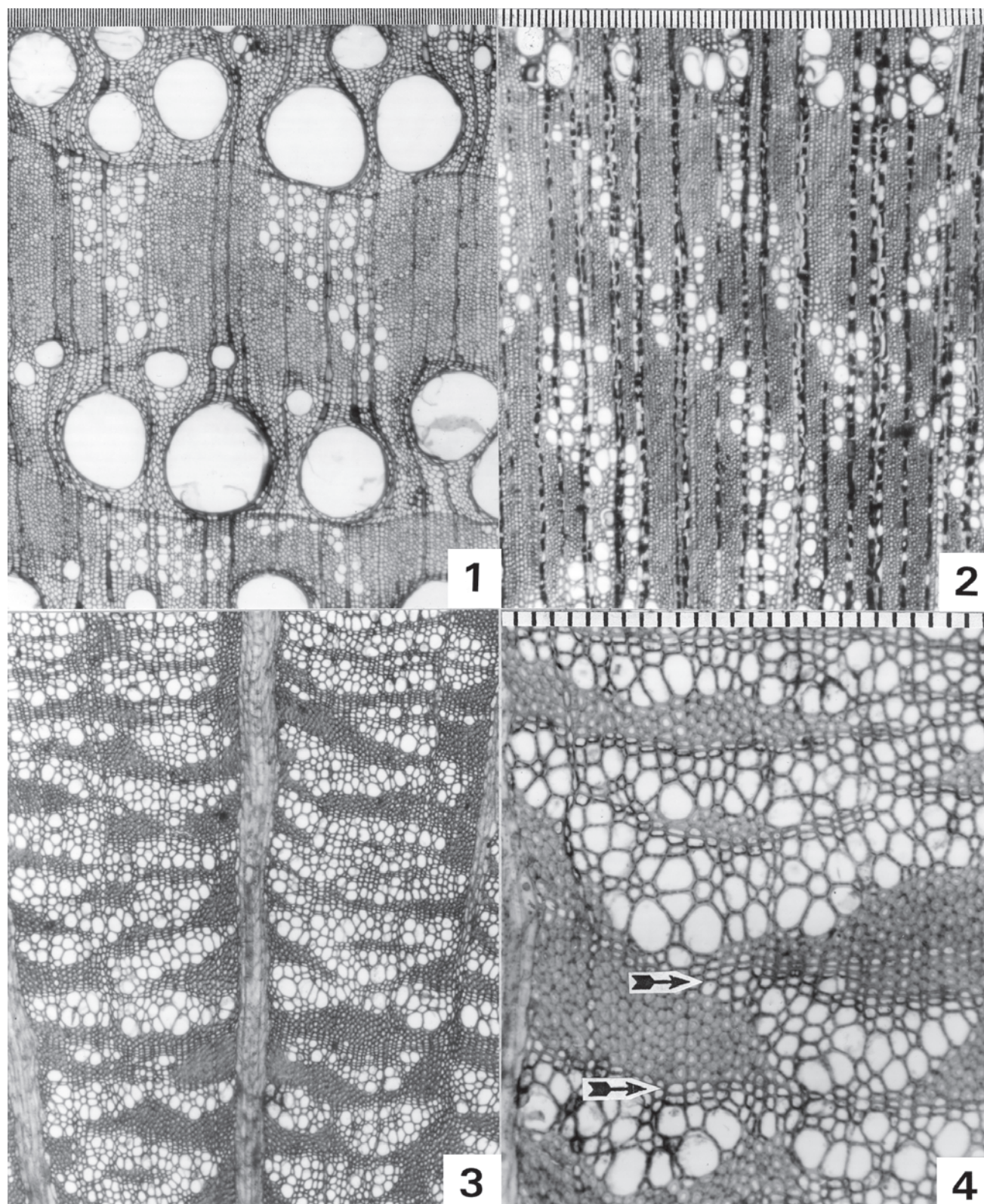


Fig. 1-4. Vessel patterns in transverse sections of dicot woods.—1. *Quercus chrysolepis* Liebm.; vessels are solitary but distributed within diagonal bands of vascentric tracheids.—2. *Ceanothus leucodermis* Greene; vessels are grouped into diagonal bands together with vascentric tracheids and parenchyma cells; earlywood at top of photograph.—3-4. *Grevillea rosmarinifolia*.—3. Vessels are grouped into tangential bands unrelated to growth rings.—4. Axial parenchyma occurs on the abaxial faces of the bands; the bands are composed of vessels and vascentric tracheids. Arrows indicate groups of axial parenchyma cells. Fig. 1, scale above Fig. 1 (divisions = 10 μ m); Fig. 2-3, scale above Fig. 2 (divisions = 10 μ m); Fig. 4, scale above Fig. 4 (divisions = 10 μ m).

these suggests the action of regulatory genes rather than a long history of change in structural genes. Vessel grouping changes over time as juvenile conditions yield to adult conformation (Lahaye et al. 2005). Reconfigurations and diversifications in characters other than non-random vessel distribution have been described in the cases of ray parenchyma (Kribs 1935), axial parenchyma (Kribs 1937), fiber dimorphism (Carlquist 1958), vessel dimorphism (Carlquist 1980), tracheid dimorphism (Carlquist 1988b), and growth ring patterning (Carlquist 1980). The physiological implications of these various reconfigurations in wood histology are suggested by comparative anatomical studies in which ecology of the plant is known, but experimental studies will help us understand these in detail. In order to understand the significance of variations in any of these categories of histological change, however, we must be aware what the patterns of diversity are. The present paper is devoted to exploring this diversity and offering avenues for future investigation.

MATERIALS AND METHODS

Plant Material

The collection data for wild and cultivated species illustrated and discussed here can be found in Appendix 1.

Terminology

The term “vasicentric tracheid” is used to denote a fibriform cell with fully bordered pits adjacent to a vessel in a wood that also contains libriform fibers or fiber-tracheids (Carlquist 1988a). This usage accords with the findings of Rosell et al. (2007). IAWA Committee on Nomenclature (1989) recognizes only cells with distorted shape under this category. Cells with such distorted shape are found adjacent to large vessels in *Quercus* L. and some Myrtaceae, in which vessel enlargement is responsible for that shape.

Latewood with narrower vessels in these species mostly has ordinary fibriform tracheids adjacent to the vessels. Myrtaceae with narrower vessels (*Melaleuca* L., *Verticordia* DC.) have vasicentric tracheids all of which have ordinary fibriform shape. The term “tracheid” follows the concept of Metcalfe and Chalk (1950), who describe tracheids as “fibers with fully bordered pits,” and agrees with IAWA Committee on Nomenclature (1964). Tracheids are thus conductive cells, in contrast to fiber-tracheids and libriform fibers (Carlquist 1988a). This concept for “tracheid” is important in the present paper because of correlations between conductive cells of the xylem and the histological plans of wood. Use of the IAWA Committee on Nomenclature (1989) definitions does not permit these functional distinctions to be made. The terms “dendritic” and “flameliike” for vessel patterns as seen in transection (IAWA Committee on Nomenclature 1989) are rejected in favor of “diagonal” bands. The terms “successive cambia” and “interxylary phloem” (formed from a single cambium) are used in accordance with Pfeiffer (1926), Obaton (1960), Carlquist (1988a, 2001a, 2007a,b), and others; IAWA Committee on Nomenclature (1989) conflates these terms.

The term “cable construction” was probably first used by Müller (as cited in Haberlandt 1914: 690). Müller hypothesized that the cable-like distribution of vascular strands in some lianas places the vital conductive cells in relatively strong

(sometimes fiber-surrounded) strands in a soft parenchyma background capable of sustaining torsion. This latter characteristic was affirmed experimentally by Putz and Holbrook (1991), who found that lianas withstood more torsional stress before water conduction was halted than did stems of a similar diameter with an ordinary wood pattern. Although dicot lianas often exemplify some type of cable construction, monocot stems represent definitive examples of this concept.

DESCRIPTIONS OF PATTERNS

Any kind of grouping of vessels within secondary xylem, as seen in transection, may be considered a non-random pattern of vessel distribution. Familiar types of vessel grouping are not considered in detail. Types of vessel grouping, cable construction, vessel spacing, and vessel absence that have not been considered in detail in the literature are described below. The descriptions below are intended as a conceptual guide, rather than an exhaustive catalog. Obviously, non-random placements of vessels are three-dimensional in nature. For convenience of a survey, transectional views are used here.

Diagonal Bands of Vessels

Similarities between the patterns in *Quercus* (Fig. 1) and the finer-scale diagonal patterns seen in *Ceanothus* (Fig. 2) and other Rhamnaceae need to be stressed. In *Quercus*, the large size of earlywood vessels may seem to set them apart from the latewood patterns in which vessels do form more easily recognizable diagonal vessel bands. If one views a transection of *Quercus* wood (Fig. 1) at a lower magnification, the diagonal patterns become apparent. To be sure, vasicentric tracheids are abundant in the bands in *Quercus* wood, making the bands seem less coherent. In *Ceanothus* (Fig. 2), vasicentric tracheids are less abundant. Vasicentric tracheids are relatively abundant in diagonal bands of some species of Rhamnaceae. Rosell et al. (2007) find that there is a continuum between the type shown here for *Quercus* and that of *Ceanothus*. The IAWA Committee on Nomenclature (1989) definition only includes certain instances of more abundant vasicentric tracheids, as in *Quercus*, Myrtaceae, and some Sapotaceae. As mentioned in Materials and Methods, the more inclusive usage of the term is employed here. A review of the phenomenon of diagonal bands of vessels in dicot woods is given by Carlquist (1987). One must keep in mind that the restriction of vessels to diagonal bands may also be viewed as a restriction of fibers to the spaces between the vessel bands. The diagonal bands of vessels include at least a few vasicentric tracheids as well as axial parenchyma and vessels of various diameters (Carlquist 1985c, 1987).

Tangential Bands of Vessels

The occurrence of tangential bands of vessels (interspersed with tangential bands of libriform fibers or fiber-tracheids) has not been noted in connection with the phenomenon of diagonal bands. The two phenomena are, however, very closely allied. The tangential bands of vessels of *Grevillea rosmarinifolia* (Fig. 3) are not related to growth rings. Numerous tangential bands are formed per year (*G. rosmarinifolia* does not have well-defined growth rings). As with diagonal bands of vessels, the tangential bands in *G.*

rosmarinifolia contain vasicentric tracheids and vessels of various diameters (the narrowest are fibriform vessels). Each of the bands also contains axial parenchyma, mostly abaxial in distribution (Fig. 4).

The systematic occurrence of tangential bands of vessels has not been tabulated, to my knowledge. Such bands occur in Proteaceae other than *Grevillea* R.Br., although they are absent in Proteaceae that have tracheids as the background cell type (e.g., *Protea* L.) rather than fiber-tracheids or libriform fibers. Small vessels embedded in tangential bands of fibriform vessels that are as narrow as tracheids are reported by Metcalfe and Chalk (1950) in such Fabaceae as *Dioclea* Spreng., *Halimodendron* Fisch. ex DC., *Spartium* L., *Ulex* L., and *Wisteria* Nutt.; these bands include a few vasicentric tracheids.

The latewood vessels of some dicotyledons (e.g., Ulmaceae) occur in tangential bands (with tendencies toward diagonal orientation in some instances). In terms of physiological adaptation, such bands may be equivalent to the tangential bands of *Grevillea* and therefore can be considered as representing this type of grouping.

Median Radial Bands in Shrubs and Subshrubs

This term is used to describe vessel groupings in which vessels occupy the central portion of a fascicular area, as seen in transection. Few or no vessels are in contact with rays: libriform fibers or fiber-tracheids intervene between a vessel band and a ray (Fig. 5–9). This pattern is not to be confused with vessels in “radial multiples” (a radial series of vessels in contact) or “radial chains” (a radial series of vessels, with imperforate tracheary elements); in these types, contact between rays and vessels are occasional, and placement of the vessels within the fascicular areas deviates to various degrees from median, as in Chloanthaceae (Carlquist 1981) and most Brassicaceae (Carlquist 1971). All of the species described under this heading can be called shrubs or subshrubs. In some species of Brassicaceae s.l., the median radial bands are characteristically present (*Isomeris* Nutt., Fig. 5) but not conspicuous.

Median radial bands were first noticed as a distinctive pattern in Papaveraceae (Carlquist and Zona 1988a). Papaveraceae do not all have median radial bands of vessels in woods, but many of them do. *Dicentra chrysantha* Walp. clearly exemplifies median radial bands because several layers of libriform fibers separate vessels from rays at most points (Fig. 6). This may also be seen in *Argemone fruticosa* Thurber ex A.Gray (Fig. 7). In *A. fruticosa*, the areas of narrow latewood vessels are tangentially wider than the areas of earlywood vessels, but several layers of libriform fibers intervene between vessels and rays. The libriform fibers are thick walled, making the separation of the vessels from the rays clearly evident (Fig. 7). *Valeriana glauca* Poepp. ex DC. (Fig. 8) shows a pattern like that of *Argemone fruticosa*, but the areas of earlywood vessels are wider tangentially, the zones of latewood vessels are narrower tangentially. Median vessel bands in *Xanthorrhiza apiifolia* L'Hér. (Fig. 9) are flanked with unusually wide rays.

Cable Construction in Lianas with Wide Rays: Variations in Median Radial Vessel Bands

One way in which a wood can be converted from a solid woody cylinder to cable construction (vessels or vessel groups

surrounded by fibrous sheaths, the fibrous sheaths isolated from each other by parenchyma) is shown in *Clematis*. The various species all have wide rays, but show various forms of distribution of libriform fibers and axial parenchyma.

Clematis haenkeana C. Presl (Fig. 10) shows vessel areas that are narrower tangentially in latewood than in earlywood. The earlywood often consists of one large vessel per fascicular area. A median radial band configuration is evident not so much in terms of vessel placement as in the conspicuous pairs of latewood fiber bands.

Vessels do not touch rays in *C. iringaensis* Engler (Fig. 11); either fibers or axial parenchyma separate vessels from rays. In *C. iringaensis*, the fiber bands do not bear a constant relationship to either latewood or earlywood. The median radial band pattern of vessels is less evident than in *C. haenkeana* (Fig. 10). Both species suggest the distribution of axial parenchyma and libriform fibers, respectively, as strands. The cable construction principle is realized, if incompletely, in these distributions.

In *Clematis alpina* L. Mill. (Fig. 12), libriform fibers have been replaced by vasicentric fibers and axial parenchyma. Note should be taken of the unusually wide rays composed of thin-walled cells. The entirety of a fascicular secondary xylem wedge between two rays can be considered a unit of cable construction, more likely to be displaced than to fracture under torsion.

Radial median patterns of vessels occur in *Polygonum baldschuanicum* Regel (Fig. 13), a woody vine. The wide rays and large vessels of *P. baldschuanicum* are familiar characteristics of woody vines, but if one looks closely, one sees that vessels rarely are in contact with rays. Likewise, one can see the median radial vessel pattern in *Vitis vinifera* (Fig. 14): at least a few libriform fibers lie between nearly all vessels and a nearby ray.

Cayratia (Fig. 15), also of Vitaceae, resembles *Vitis* L. in transectional wood pattern, but with some significant differences. Rays are composed of very thin-walled, non-lignified parenchyma. Axial parenchyma is distributed in a way that coordinates with sheathing of vessels and vessel groups. Comparing *Vitis* (Fig. 14) and *Cayratia* (Fig. 15), one sees median-band vessels in the former with fiber-sheathed vessels in the latter.

Coccinia (Fig. 16) of Cucurbitaceae provides an example in which large vessels are almost individually sheathed in fibers, and the remainder of the secondary xylem consists of thin-walled non-lignified parenchyma.

Cable Construction in Lianas: Woods Lacking Wide Rays

A common textbook figure of lianoid structure in woody dicots is based on *Bauhinia*, a commonly occurring liana in neotropical and paleotropical areas. Illustrations of transections show irregular fibrovascular strands in a parenchymatous background (e.g., Solereder 1906). The central theme of this type of construction is an increase in axial parenchyma distribution so as to isolate groups of vessels sheathed in fibers. An incipient form of this tendency is represented by *Thunbergia laurifolia* Lindl. of Acanthaceae (Fig. 17). *Thunbergia laurifolia* is rayless, but larger zones of axial parenchyma separate the fiber-sheathed vessels. There are smaller vessels, some not much wider than fibers, associated with the

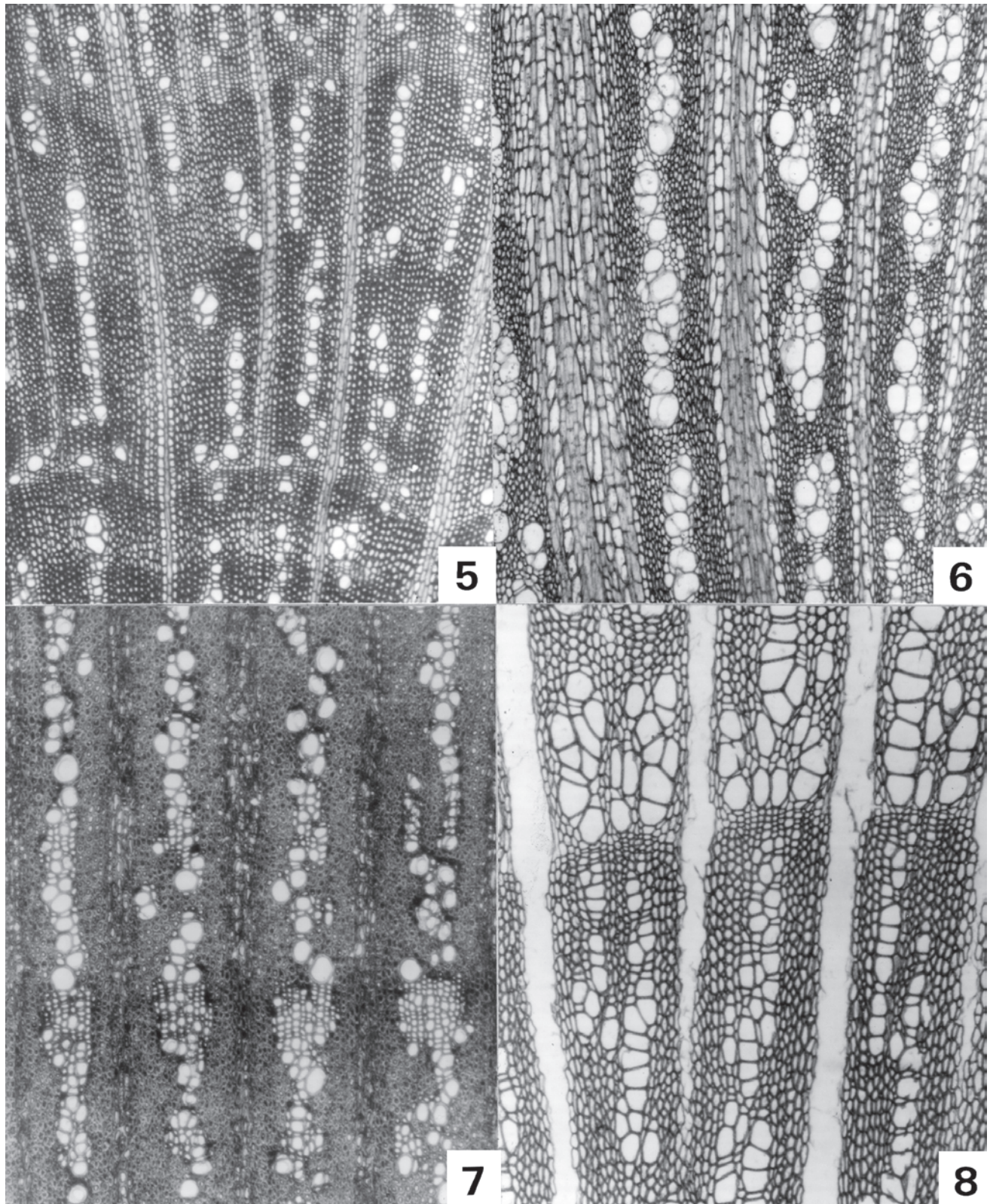


Fig. 5-8. Transections of dicot woods with median radial bands of vessels.—5. *Isomeris arborea* (cult. Rancho Santa Ana Botanic Garden).—6. *Dicentra chrysantha*.—7. *Argemone fruticosa*.—8. *Valeriana glauca* (Carlquist 7260, RSA). Scale for Fig. 5-8 above Fig. 2.

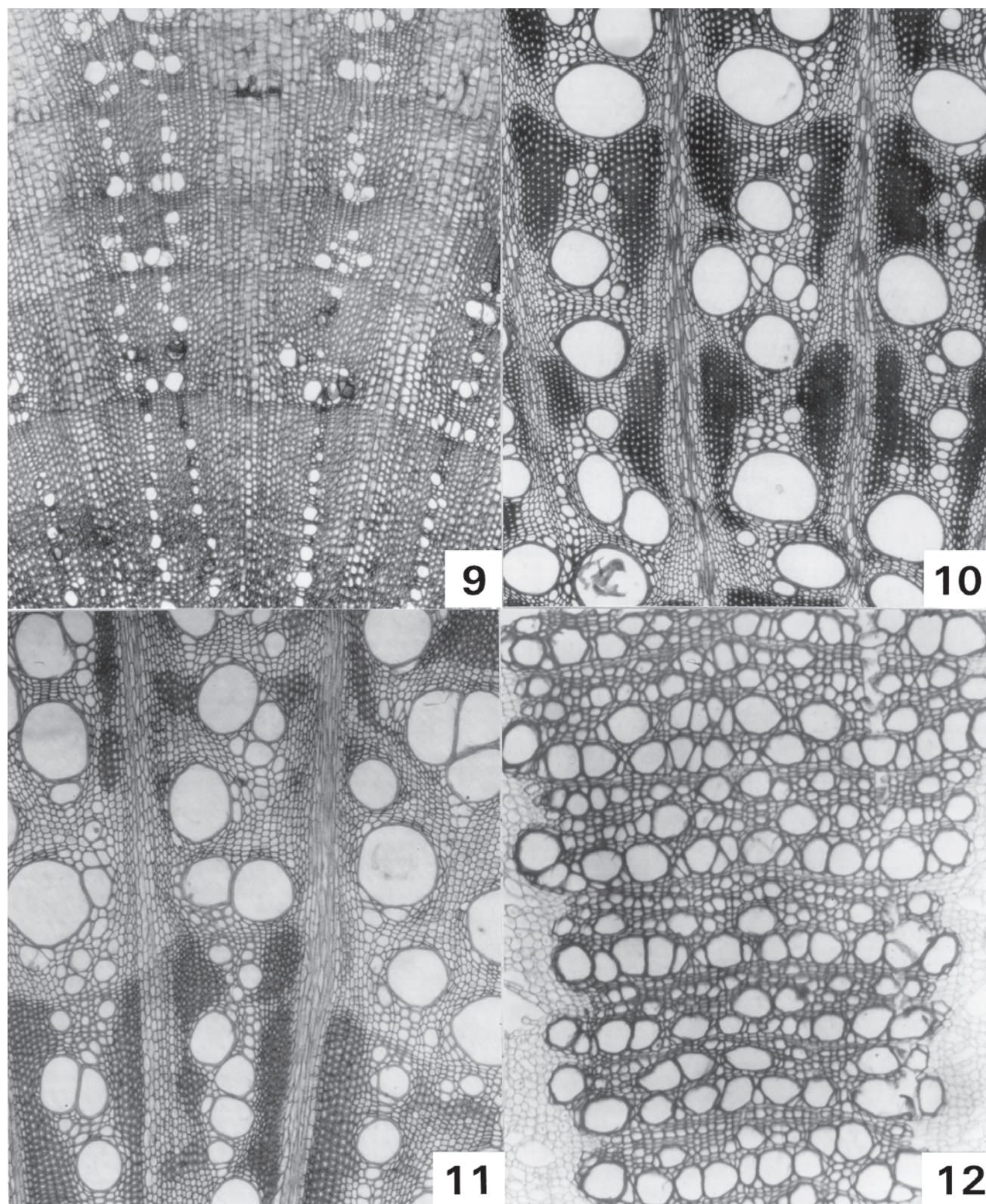


Fig. 9–12. Transections of woods of Ranunculaceae.—9. *Xanthorhiza apiifolia*.—10. *Clematis haenkeana*.—11. *Clematis iringaensis*.—12. *Clematis alpina*. Fig. 9, 12, scale above Fig. 2; Fig. 10–11, scale above Fig. 1.

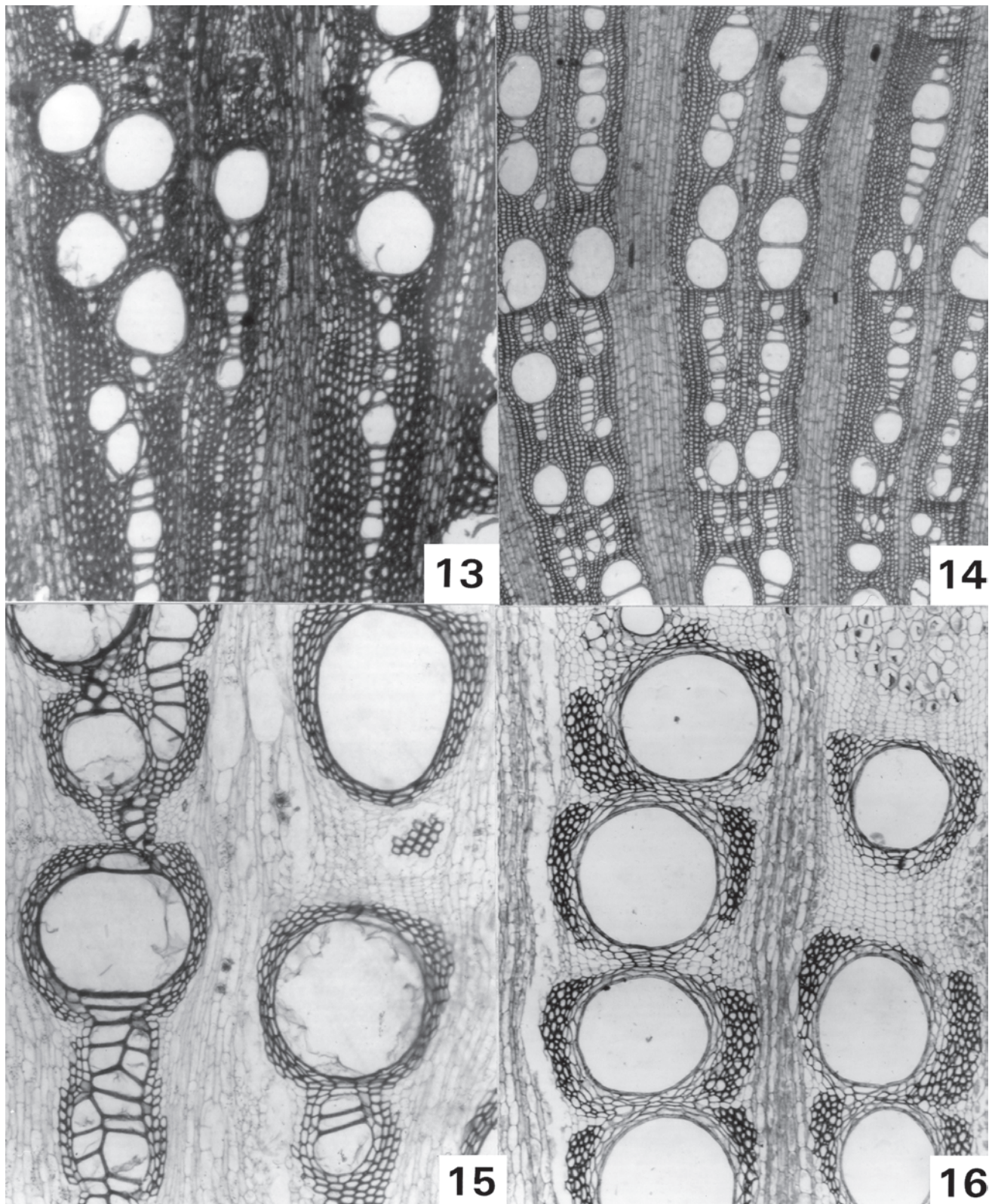


Fig. 13–16. Transsections of stems of lianoid dicots.—13. *Polygonum baldschuanicum*.—14. *Vitis vinifera*.—15. *Cayratia* sp.—16. *Coccinia grandis* (L.) Voigt. Fig. 13, scale above Fig. 2; Fig. 14–16, scale above Fig. 1.

larger vessels. Clearly this pattern represents a non-random form of vessel distribution. Larger strands of axial parenchyma contain phloem (interxylary phloem formed from a single cambium, not phloem formed from successive cambia). The phloem is not readily stained and so is not clearly visible in Fig. 17. Thin, tangentially oriented bridges of fibers interconnect some of the fiber-sheathed vessels and vessel groups in *T. laurifolia*. A number of these tangential bridges break as the stem enlarges in diameter.

Mendoncia microchlamys Leonard (Fig. 18) might be expected to be similar in structure to *Thunbergia laurifolia*; both belong to Acanthaceae and are lianas (*Mendoncia* is sometimes recognized in a separate family). However, the structure of *M. microchlamys* is quite different. *Mendoncia* has successive cambia: fascicular zones originate from multiple sites of origin, rather than from a cylindrical master cambium (the latter, for example, would be found in *Beta* L.). Narrow rays are present within the fascicular areas. Parenchyma areas within the fascicular areas shown are clearly present; they often show cellular proliferation that fragments the strand into segments. Phloem strands do not occur within the axial parenchyma. Phloem is abundant and tends to surround the fascicular areas as they enlarge: fibers are scattered within the secondary phloem and serve as convenient markers for phloem presence (Fig. 18, right). These patterns have been reported for the closely related genus *Afromendoncia* Gilg ex Lindau by Obaton (1960). Obaton figures repeated fragmentation of fascicular areas, so that cable construction is multiplied over time.

Convolvulaceae, which have predominantly narrow rays, show various degrees of cable construction. *Breweria menziesii* Benth. & Hook f. (Fig. 19) illustrates some early stages in introduction of axial parenchyma into the fascicular xylem. Bands of parenchyma, some diagonally oriented, dissect the woody cylinder into segments of various sizes. The abundance and size of these parenchyma bands increases with age of stem.

Operculina palmeri House (Fig. 20) represents a more definitive version of cable construction. The bands of parenchyma tend to isolate the large vessels individually. Cells that appear to be fibers tend to form arcs abaxial to each of the large vessels. In fact, the background tissue of wood in Convolvulaceae consists of fibriform vessels and tracheids. An exception occurs in shrubby Old World species of *Convolvulus* L., in which the background cells are thick-walled tracheids (Carlquist and Hanson 1991). In *Ipomoea tiliacea* Choisy, the separation of vessels and their sheathing tracheary elements as individual units is even greater, so that cable construction is definitively achieved (Carlquist and Hanson 1991).

Vessel Patchiness in Vines and Lianas

Vessel patchiness is a term applied here to a non-random vessel distribution pattern in which vessels are confined to particular areas of secondary xylem. Large areas of secondary xylem may be devoid of vessels in this pattern. This configuration was noted earlier for Convolvulaceae by Carlquist and Hanson (1991). Vessel patchiness is well illustrated by *Ipomoea fistulosa* Mart. ex Choisy (Fig. 21, 22). Vessels may occur in zones that are about as wide tangentially as radially (Fig. 21). Vessels may be arranged in radial strips (Fig. 22). The majority of species of *Ipomoea*,

including the ones presented in Fig. 21–24, have successive cambia (Carlquist and Hanson 1991). Two vascular increments are shown for *I. pauciflora* M. Martens & Galeotti in Fig. 23. These vascular increments have a tendency for production of tracheids first, then vessels later. Production of axial parenchyma also increases during the functioning of a given vascular cambium. Thus, strands of vessels and associated tracheids tend to be surrounded by varying quantities of axial parenchyma. Most species of *Ipomoea* have relatively narrow rays (Carlquist and Hanson 1991).

The presence of wide rays in *I. arborescens* G. Don subsp. *glabrata* (A. Gray) Gentry (Fig. 24) results in a heightened form of vessel patchiness: some fascicular xylem areas between a given pair of rays may lack vessels entirely (Fig. 24, right), while other fascicular xylem wedges contain vessels.

Patchiness of vessels in the sense of the examples in Fig. 21–24 has been illustrated by Bailey and Howard (1941) and Metcalfe and Chalk (1950) for the following species: Convolvulaceae: *Calystegia sepium* (L.) R. Br.; Icacinaceae: *Hosiea sinensis* (Oliv.) Hemsl. & Wats., *Iodes* Blume spp., *Pyrenacantha repanda* Merr.; Loganiaceae: *Strychnos atherstonii* Haw.; and Passifloraceae: *Passiflora racemosa* Brot.

All of the species in this list are lianoid. *Urtica dioica* L. appears to have patchy vessels in the figure by Metcalfe and Chalk (1950), but it is probably not homologous with the instances cited above. Bands of unlignified fibers occur in the radial secondary xylem zones that lack vessels in *U. dioica*, and the construction of these bands is unlike the wood plans of the lianas mentioned above.

Non-Random Vessel Distribution Related to Succulence

Succulence does not by itself result in non-random distribution of vessels. However, the patterns of vessel distribution in some succulents involve displacement of parenchyma as well as fibrous tissue in order to facilitate expansion and contraction with changing water storage amounts.

Misodendrum (Misodendraceae) exhibits normal cambial growth except that a second series of bundles can originate in the pith of stems of *M. brachystachyum* DC. (Fig. 25) and *M. quadrifolium* DC. Secondary growth occurs in the stems of all species (Carlquist 1985b), contrary to the implication of the use of the word “bundles” by Metcalfe and Chalk (1950) for the fascicular areas of *M. brachystachyum*. The stem does feature wide rays that consist of thin-walled cells. The rays are part of the secondary growth, but because their radial increase in size is aided more by cell elongation than cell division, they resemble primary rays to some degree. The fascicular areas of *M. brachystachyum* and *M. oblongifolium* DC. (Fig. 26) feature pairs of libriform fiber strands in characteristic patterns in latewood. In some cases, the two strands of a pair are fused (Fig. 26, bottom). The contrast between the thin-walled axial parenchyma and the thick-walled fibers is striking, but both of these distinctive tissues are portions of the secondary xylem.

A reverse tendency, conversion of the background as well as rays into fibers, is illustrated by *M. punctulatum* Banks ex DC. (Fig. 27). The pattern of vessel distribution—tangentially wider zones of vessels in earlywood, tangentially narrower zones of vessels in latewood—is actually the same as in *M.*

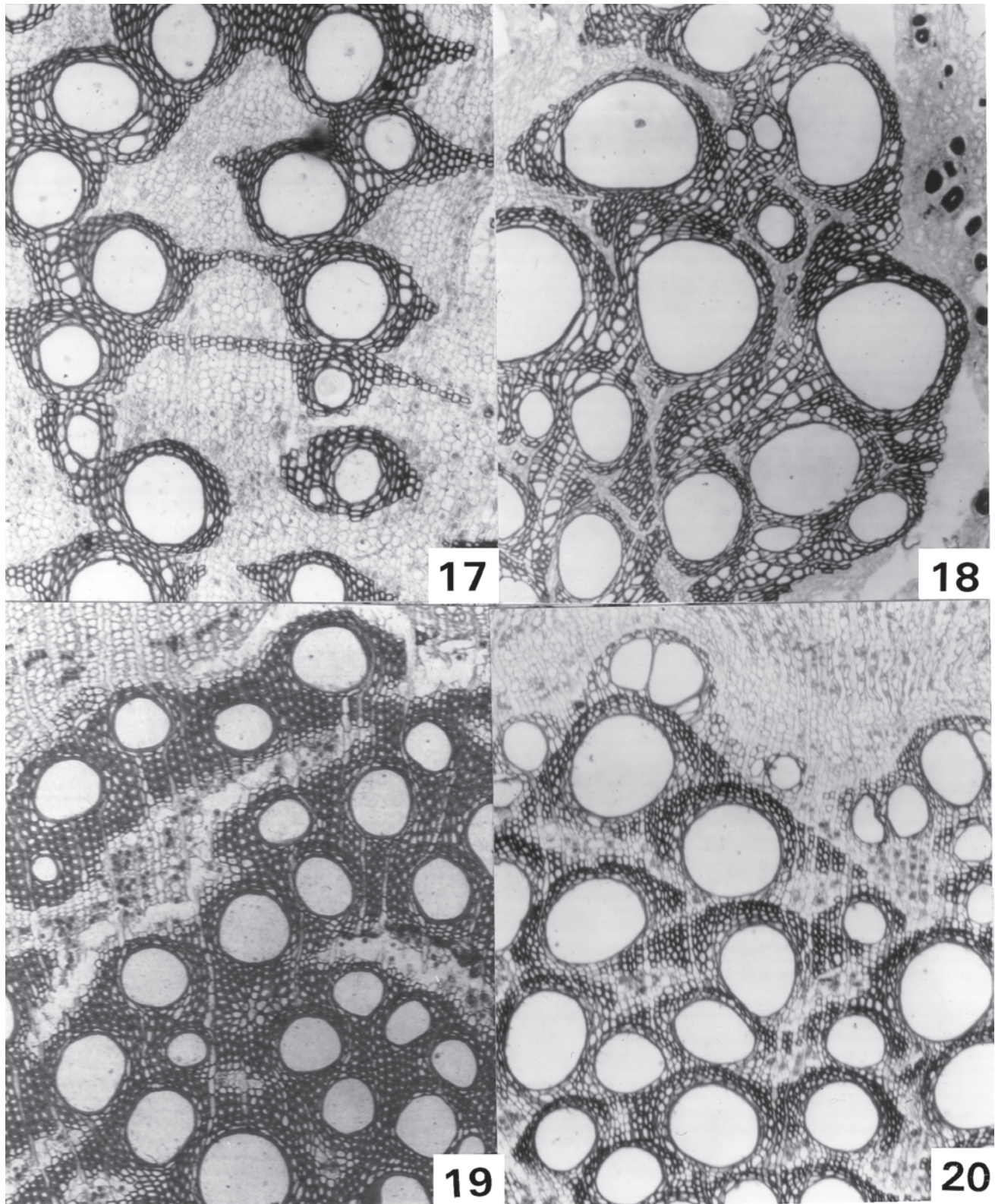


Fig. 17–20. Transections of stems of lianoid dicots.—17. *Thunbergia laurifolia*.—18. *Mendoncia microchlamys*.—19. *Breweria menziesii*.—20. *Operculina palmeri*. Fig. 17–19, scale above Fig. 2; Fig. 20, scale above Fig. 1.

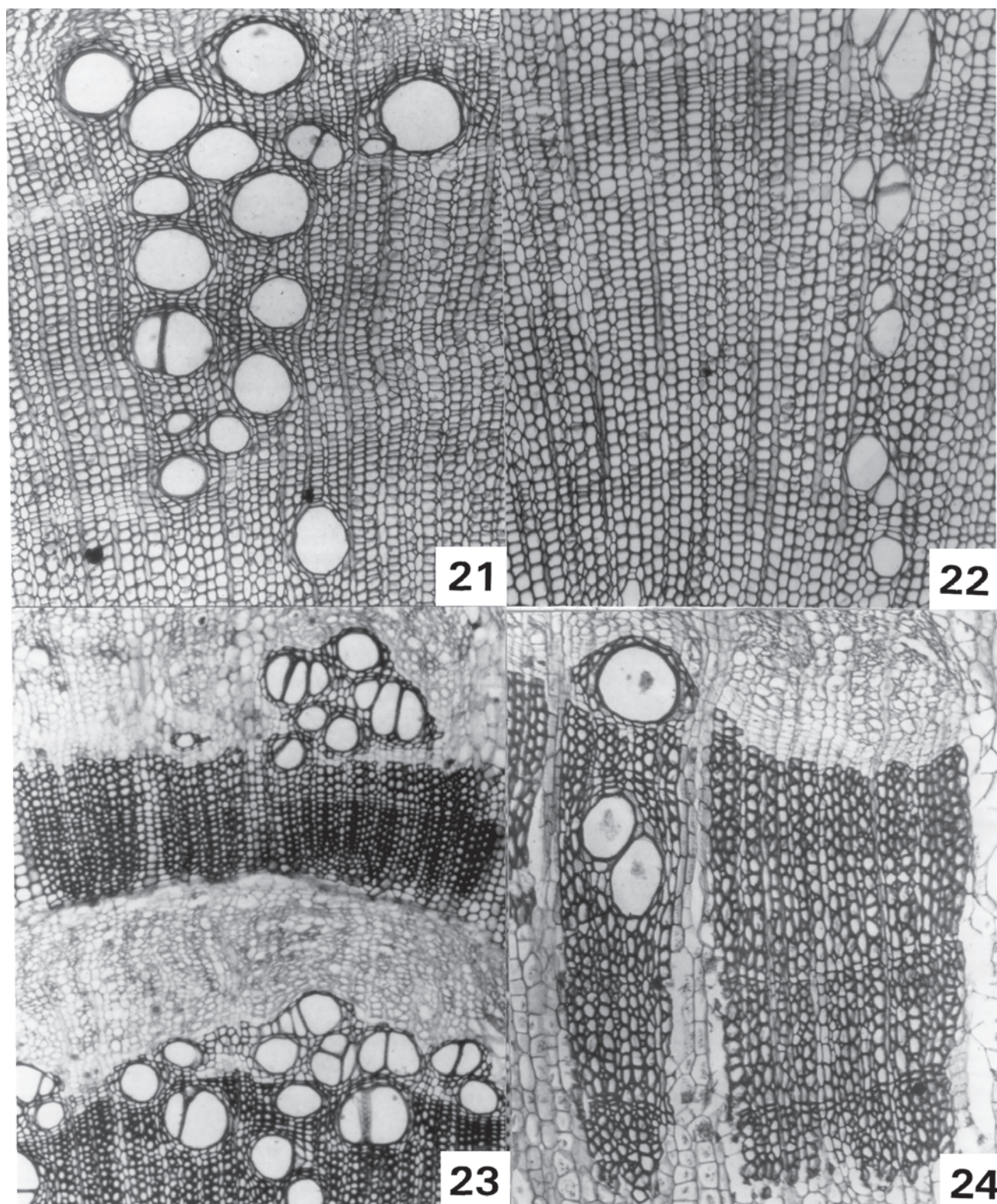


Fig. 21–24. Transections of stems of *Ipomoea* (Convolvulaceae).—21. *I. fistulosa*, section from younger stem.—22. *I. fistulosa*, section from inner older stem.—23. *I. pauciflora*.—24. *I. arborescens* subsp. *glabrata*. Fig. 21–22, 24, scale above Fig. 2; Fig. 23, scale above Fig. 1.

brachystachyum or *M. oblongifolium*. The conversion of potential ray areas to fibers indistinguishable from libriform fibers in *M. punctulatum* results in a rayless condition for this species. The stems of *M. brachystachyum* and *M. oblongifolium*

are thick and succulent, whereas the stems of *M. punctulatum* are slender and wiry.

Complete absence of libriform fibers characterizes the wood of *M. quadrifolium* (Fig. 28). Vessels in latewood are

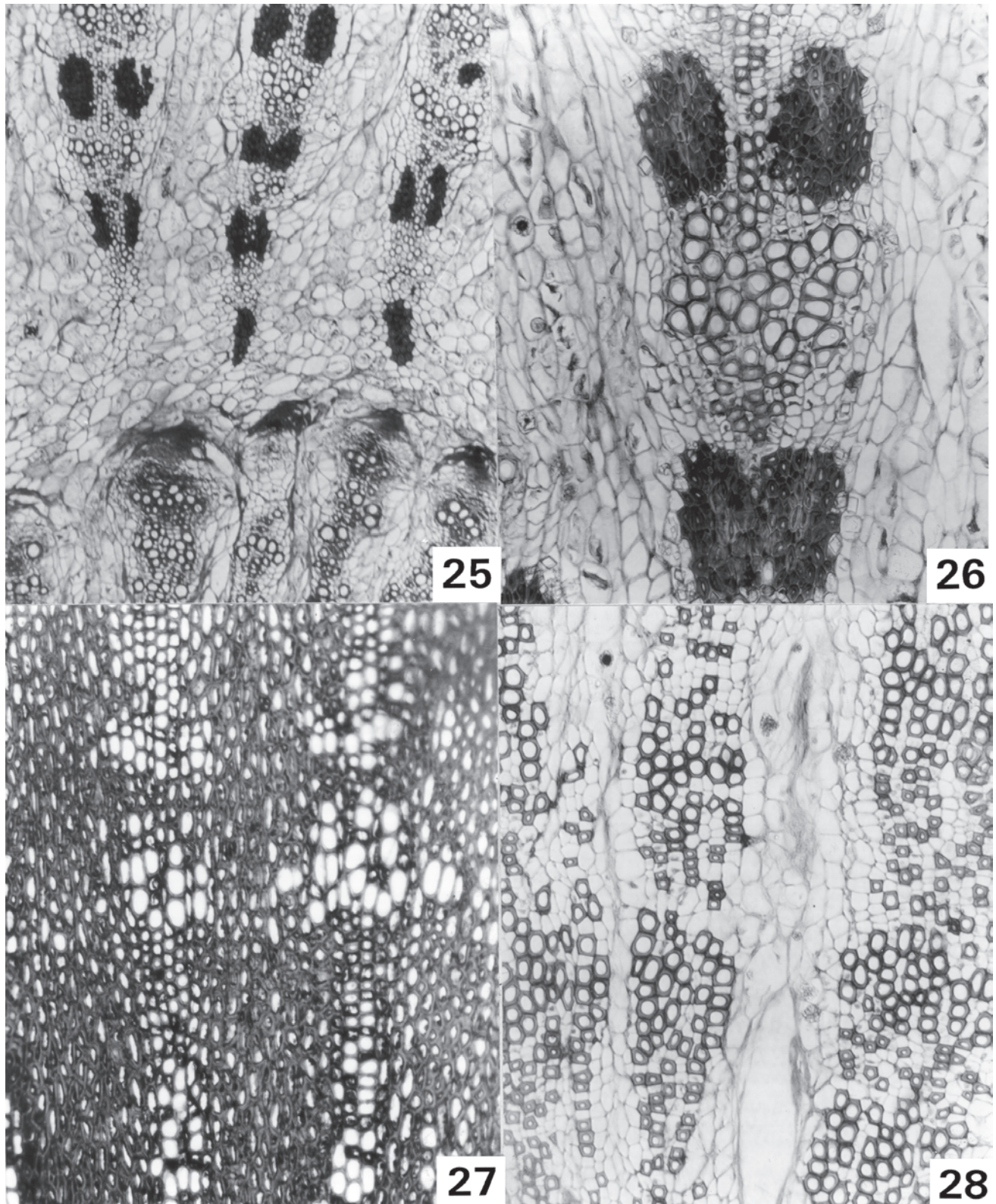


Fig. 25–28. Transverse sections of secondary xylem of *Misodendrum* (Misodendraceae).—25. *M. brachystachyum*.—26. *M. oblongifolium*.—27. *M. punctulatum*.—28. *M. quadrifolium*. Fig. 25, scale above Fig. 2; Fig. 26–28, scale above Fig. 4.

associated with more axial parenchyma than vessels in earlywood. Thus, vessel grouping in latewood is scarcer than it is in earlywood, a condition contrary to what is present in most dicot woods with growth rings.

Succulence is involved in a number of instances in which successive cambia occur, such as Aizoaceae (Carlquist 2007a). Successive cambia thus can be counted as a way of achieving parenchyma intercalation between vessel groups.

Non-Random Vessel Distribution Related to Successive Cambia

The successive cambia most commonly illustrated (e.g., *Beta*) possess concentric cylinders of vascular increments (secondary xylem and secondary phloem produced from a vascular cambium). The vascular increments are usually shown as alternating with cylinders of conjunctive tissue (produced from a master cambium: Carlquist 2007b). Rays, often wide, occur in species with successive cambia, although rays are absent in some families (Aizoaceae: Carlquist 2007a). One can argue that rays, whether in species with successive cambia or whether in single-cambium woods, do not really displace vessels, and that they merely produce minor shifts in positioning. Conjunctive tissue and secondary phloem, however, do produce significant spacings between successive cylinders of secondary xylem, and therefore between cylinders of vessels (Fig. 29). These spacings have indefinite vertical extents in a stem or root, unlike the brief vertical “interruptions” to vessel randomness provided by rays.

In analyzing successive cambia, one must keep in mind that the “ground” or “background” tissue of a stem with successive cambia is not wood. Contrary to the IAWA Committee on Nomenclature (1989) terminology, the “ground” tissue of a stem with successive cambia is really conjunctive tissue into which bands of secondary xylem and secondary phloem, produced by the successive vascular cambia, have been interpolated. One may be tempted to think otherwise for some genera (e.g., Menispermaceae) in which vascular cambia may produce very thick cylinders of secondary xylem, but even in these species, conjunctive tissue is present and must be accounted for.

Aptenia (Fig. 29) and *Mestoklema* (Fig. 30) show more numerous vessels in earlier-formed vascular increments, and few or no vessels in later-formed vascular increments (Carlquist 2007b). In such instances, there can be no doubt that vessel distributions in stems and roots are non-random. The outer increments that lack vessels are definitely vascular in nature. The number of rows of fibriform cells, when counted tangentially, is much greater than the number of rows of conjunctive cells, so the fibriform cells are libriform fibers produced by vascular cambia (sometimes secondary phloem is produced by these cambia, which do not produce vessels). Subdivision of master cambium derivatives so as to form vascular cambial initials is one of the hallmarks of successive cambium activity (Carlquist 2007b).

Conjunctive tissue in Aizoaceae can be composed of fibrous tissue, as in *Stayneria* (Fig. 31) or *Ruschia* Schwantes. *Guapira discolor* (Spreng.) Little (Fig. 32, 33) and *Pisonia rotundata* Griseb. have fibrous conjunctive tissue, but also thin-walled conjunctive tissue parenchyma. The latter forms arcs or caps external to the secondary phloem strands. Rays are present in *Guapira discolor* and *Pisonia rotundata*, but the rays are

produced, contrary to what one might assume, by the master cambium, not by the vascular cambia (for detailed ontogenetic analysis of this phenomenon, see Carlquist 2004, 2007b). Interestingly, the absence of rays in the vessel groupings and the secondary phloem strands confirms that the vessels and secondary phloem are produced from vascular cambia, whereas the rays as well as the fibrous and parenchymatous conjunctive tissues are produced by the master cambium. Thus the vessel distributions in the stems of these species are non-random as a result of this unusual ontogenetic scheme.

Vessel Sparsity or Absence Within Growth Rings

The growth ring phenomenon chosen for emphasis here is one that does not involve grouping of vessels. In Fig. 34, one can see that the last several rows of growth rings of *Myrica peregrina* Kuntze are tracheids; the end of the growth ring lacks vessels. This growth ring type was termed Type 5B by Carlquist (1980, 1988a, 2001a). The absence of vessels from the last several cell layers of latewood is consistent throughout growth rings of this species and those of other unrelated dicotyledon species, such as many Ericaceae and Rosaceae (Carlquist 1980).

Myrica hartwegii S. Watson (Fig. 35) corresponds to Type 5A (Carlquist 1980, 2001a). The background tissue in both *M. peregrina* and *M. hartwegii* consists of tracheids. In *M. hartwegii*, the tracheids form most of the growth ring, and vessels are restricted to earlywood (Carlquist 2002).

Growth rings occur in globular cacti. The growth ring illustrated for *Mammillaria mystax* (Fig. 36) is typical. Vessels are present in the first portions only of the earlywood. The remainder of the growth ring consists of tracheids—perhaps best termed vascular tracheids. Vascular tracheids of globular cacti have wide helical bands. Vessel elements have similar but narrower bands. In addition, vessels may be distinguished from vascular tracheids by the presence of axial parenchyma cells among them (“intervascular parenchyma”). Vessels are about the same diameter as vascular tracheids, but can be distinguished from them (Fig. 37) by the two features cited. The growth rings of globular cacti are referable to Type 5A. Type 5 growth rings, although common in some dicotyledons that have tracheids as a background cell type, are also notably present in *Ephedra* L. (Carlquist 1989, 1992b).

Type 5 growth rings feature absence of vessels from part or all of the latewood. This is obviously a non-random distribution. The presence of vascular tracheids at the end of a growth ring that features vessels and libriform fibers in earlywood can also be considered as absence of vessels in the last one or two layers of latewood, and thus a histological phenomenon very similar to Type 5 growth rings.

Interxylary Phloem

Interxylary phloem (strands or bands of phloem and associated parenchyma produced inwardly from a single cambium) represent various degrees of displacement of vessels from a random pattern in secondary xylem. Examples include various genera of Icacinaceae (*Chlamydocarya* Baill., *Phytocrene* Wall., *Sarcostigma* Wight & Arn.: Bailey and Howard 1941), *Strychnos* L. (Metcalf and Chalk 1950), and various Myrtales such as Combretaceae and Onagraceae (for a full listing, see Carlquist 2001a: 282). Interxylary phloem strands

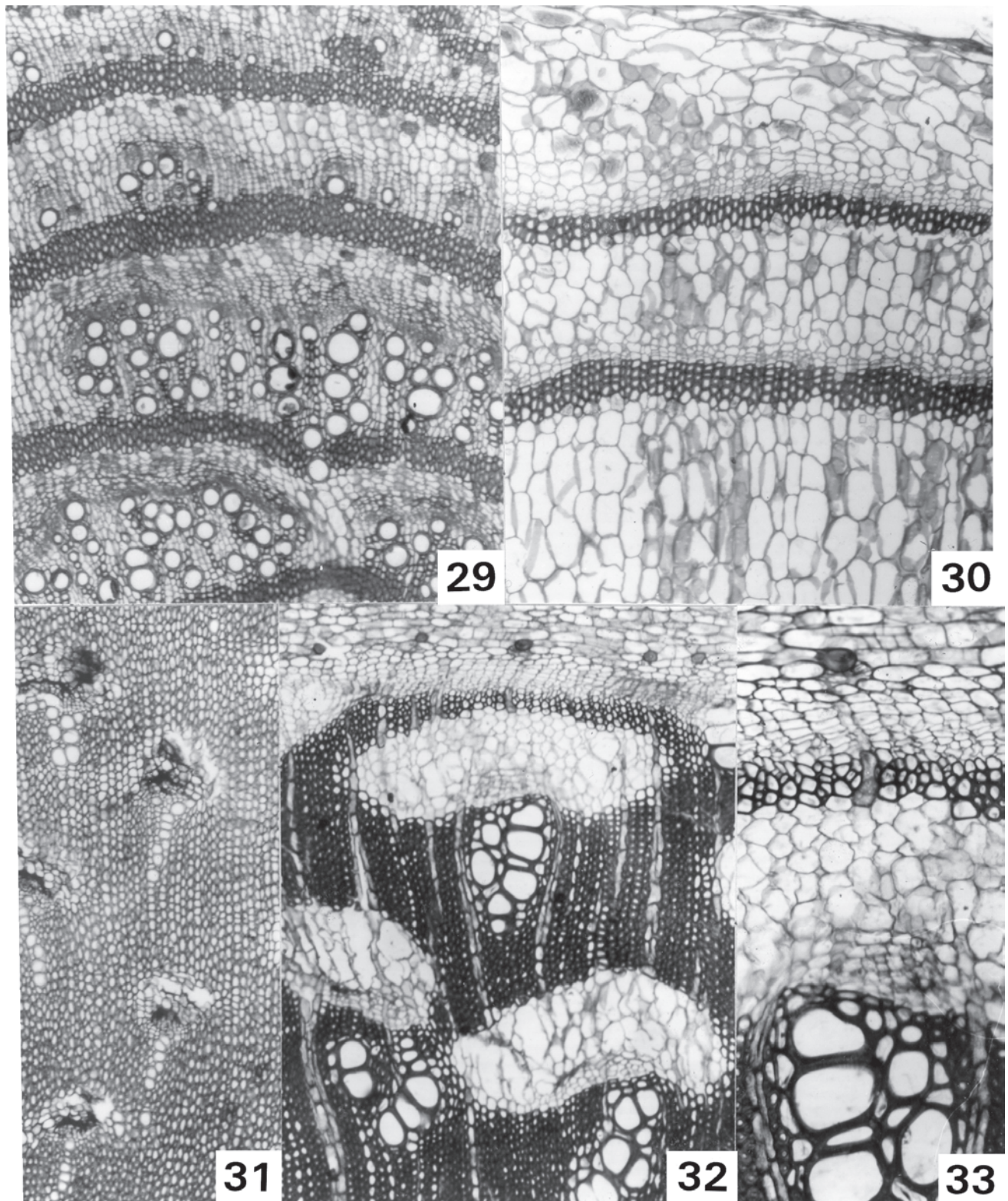


Fig. 29–33. Transections of dicot stems with successive cambia.—29–31. Aizoaceae.—29. *Aptenia cordifolia* (L.) Schwantes.—30. *Mestoklema tuberosum* (L.) N.E.Br.—31. *Stayneria neilii* (L.Bolus) L.Bolus.—32–33. *Guapira discolor* (Nyctaginaceae).—32. Portion to show three vascular increments.—33. Portion to show several vessels and, above them, a strand of secondary phloem (dark gray) derived from the same vascular cambium as the vessels. Fig. 29–32, scale above Fig. 2; Fig. 33, scale above Fig. 4.

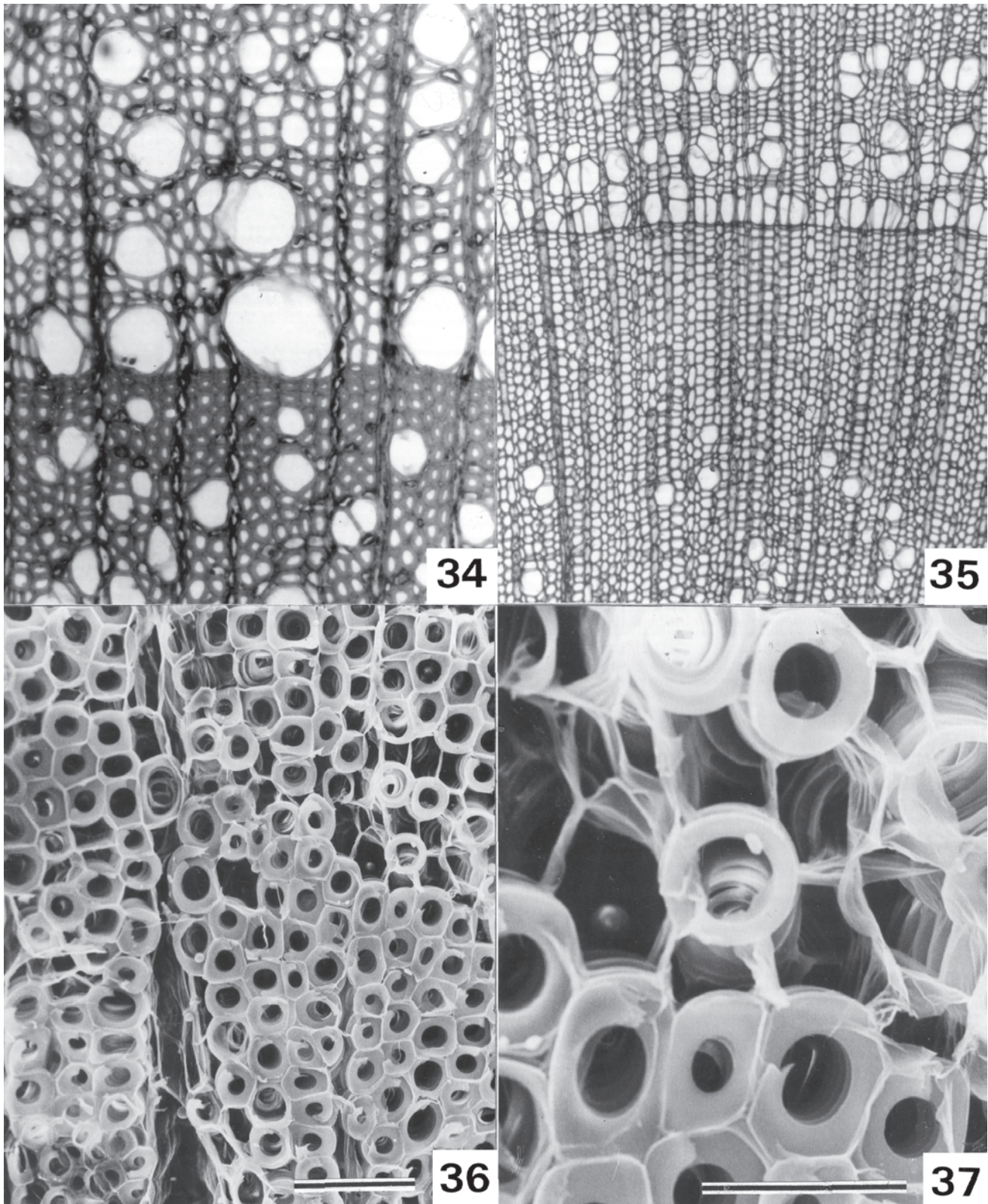


Fig. 34–37. Transections of secondary xylem of Myricaceae and Cactaceae.—34. *Myrica peregrina*, showing latewood of a growth ring succeeded by earlywood of the next.—35. *M. hartwegii*, latewood, much of which is vessel free, plus earlywood of the next growth ring.—36–37. Transection of *Mammillaria mystax* (cultivated, Santa Barbara, CA) as seen with scanning electron microscopy.—36. Excerpt showing portions of two adjacent growth rings consisting mostly of tracheids.—37. Enlarged portion of the same section, to show vessels surrounded by parenchyma cells (upper half of photograph, narrower secondary wall bands) and tracheids (lower portion of photograph, wider helical secondary wall bands). Fig. 34, scale above Fig. 4; Fig. 35, scale above Fig. 2; Fig. 36, scale = 100 μ m; Fig. 37, scale = 50 μ m.

are vertically of indefinite length, and thus are in a different category from rays, which represent minor detours in vessel pathways and therefore do not create non-randomness. Admittedly, the studies examining three-dimensional patterns in interxylary phloem are few (Pfeiffer 1926).

DISCUSSION AND CONCLUSIONS

Vessel Grouping and Its Physiological Significance

Comparative wood anatomy demonstrates that if vessels are embedded in a background of tracheids or abundant vasicentric tracheids, vessel grouping is not present (Carlquist 1984). Vessel grouping is not the same concept as “redundancy” as used by Ewers et al. (2007). Those authors consider number of vessels *within* an organ as opposed to number of vessels per unit area. Neither of those concepts is the same as the one I am discussing here, which is number of vessels per vessel group (as seen in transection) independent of organ size, organ diameter, or vessel density. Thus, I propose the term “conductive pathway replication” to suggest the possible physiological value of having vessels that are in contact and theoretically would provide safety by virtue of representing a pathway in terms of several vessels rather than one large vessel. Vessel redundancy in the sense of Ewers et al. (2007) is a concept useful in explaining why twigs and branches of a given plant may die during a period of water stress, whereas the main axis of the plant can survive (Rood et al. 2000). The trunk as an organ can be expected to have more numerous functional vessels than a branch of a given plant. Vessel redundancy was analyzed theoretically by Ewers et al. (2007) as an independent variable, but of course, in real life situations vessel redundancy is never independent of vessel diameter, vessel density, vessel grouping, or background cell type. These latter four parameters are important where conductive safety (survival of a sufficient number of water columns to prevent death of an organ) is concerned.

In fact, vessel grouping is very closely related to the type of imperforate tracheary element in a wood. If a wood contains abundant vasicentric tracheids or has a fibriform background composed entirely of tracheids, vessels do not group and are notably solitary (Carlquist 1984). The inescapable conclusion is that presence of tracheids as a background tissue is a more effective strategy for preventing disabled conductive pathways (embolism spread among vessels is rare) than vessel grouping (embolisms spread from one vessel element in a vessel into another vessel element). Tracheids may have the disadvantage of being a relatively poor conductive system compared to vessels in dicots that have vessels (Zimmermann 1971). The conductive role of tracheids in dicots has not been well studied because of the difficulties in observing sap flow and embolism occurrence in such narrow conduits, and conclusions must at present be based on inferences from comparative wood anatomy. Understandably, vessels offer a much more easily observed conductive system than the tracheids that accompany them.

The Nature of Vessel Grouping

The analysis of Ewers et al. (2007) concerns vessel redundancy per organ independently of vessel density (= vessel redundancy per unit transectional area) and vessel

diameter. However, vessels vary in diameter in any wood. Experimental work shows that narrower vessels withstand embolism better than wider vessels (Huber 1935; Zimmermann 1971; Ellmore and Ewers 1985; Ewers 1985; Hargrave et al. 1995). The model of Ewers et al. (2007) shows that when vessel redundancy per organ is high (>100), “runaway cavitation” disables the conductive system. If considered on the basis of uniform vessel diameter, that model may be true. However, vessel diameter in a wood sample is never uniform: variance is often quite considerable. Comparative wood anatomy shows that large vessel groupings contain narrow vessels as well as wider ones. A high degree of vessel grouping appears advantageous in dry situations in dicot woods that have libriform fibers or fiber-tracheids as the imperforate tracheary element type (Carlquist 1966, 1983; Carlquist and Hoekman 1985). Narrow vessels and tracheids in vessel groups clearly have a role in prevention of embolism spread due to drought or freezing (Hargrave et al. 1995).

Quantitative Values for Minimal Vessel Grouping

Vessel-bearing woods with tracheids as the imperforate tracheary element type clearly do have a low degree of vessel grouping, but in my observations of various dicot woods in this category, the number of vessels per group never is as low as 1.0. The value 1.2 vessels per group is approximately the minimal value observed to date for such woods (original data). One could attribute this merely to packing constraints, and thus to random contacts between vessels. However, other possible correlations need to be considered. Explanations include the necessity for occurrence of a certain number of vessel contacts in order for the conductive system of a given wood or organ to function. Three-dimensional anastomosis among vessels, although difficult to demonstrate, does occur. One such demonstration is offered by the dye uptake patterns reported by Ewers et al. (1991). Does approximately equidistant spacing of vessels throughout a wood have a positive value in a wood? That might maximize the number of cells contacting vessel elements and achieves the greatest degree of three-dimensional spread of the water supply system within a wood. A certain number of contacts between older vessels and newer vessels must occur so that new pathways take over from old pathways in a sequential fashion as secondary growth proceeds.

Patterns of Vessel Grouping

Characteristic patterns of vessel groups as seen in wood transections have long been described by wood anatomists, but the physiological basis for the various patterns has been little studied. In effect, the patterns are relatively few. The term “vessels in multiples” is often used to cover all grouping situations. The most common tendency is a radial one. “Radial multiples” connotes vessels in unbroken radial groupings, “Radial chains” describes vessels in radial alignments, but with other cells intervening occasionally within the radial arrangements. Radial groupings may offer the most economical way of adding newer vessels to existing pathways: an outer vessel in a series is brought on line as an older vessel is decommissioned. To be sure, contacts among these radial plates must occur at some degree of frequency.

Diagonal bands of vessels offer the possibility of frequent lateral as well as radial contacts between newly added vessels and pre-existing ones. When viewed three-dimensionally, vessels, narrow vessels, and vasicentric tracheids in these bands form cohesive structures based on a continuous series of contacts. Braun (1970) showed this by means of fluorescent dye studies of *Rhamnus* L. wood. Moreover, the dye patterns show that such diagonal interlinking bands stay active in conduction for an indefinite number of years. All of the conductive pathways in a given stem are probably linked into one conductive unit in this pattern, with the narrow vessels and vasicentric tracheids serving as "safe" elements more resistant to embolism occurrence and spread. These latter two cell categories and their pattern of contacts very likely maintain the conductive system when larger earlywood vessels embolize. Typically, tyloses (an indication of vessel decommissioning) occur in earlywood but not latewood of *Quercus*.

Tangential groupings of vessels as seen in transections are occasional in dicot woods. Some, as in the latewood of *Ulmus*, in fact have a more diagonal orientation than one might think from some illustrations. Tangential vessel groupings, as shown here for *Grevillea* (Fig. 3, 4), have radial interconnections with each other and are not as different from typical diagonal bands as one might imagine. Similarly, in species with diagonal bands of vessels embedded in vasicentric tracheids (*Quercus*, *Rhamnus*), concentric tangential layers of vasicentric tracheids often occur in latewood (Carlquist 1985c); these layers laterally interconnect the vessel-bearing diagonal bands with each other (Braun 1970: Fig. 88).

The tangential, radial, and diagonal bands of vessels in dicot woods clearly are non-random placements of vessels. One is especially aware of this when one notes the accompanying vessel-free zones of fibriform cells (usually libriform fibers) in these woods. Large patches of vessel-free fibers may form a very strong distribution of mechanically strong cells. Examination of this possibility by experimental means may not be easy, but comparative stress tests on woods with various sizes of fiber columns free of vessels should be possible.

Median Radial Band Patterns: Correlations

The lack of contact between radial vessel groupings and rays, as illustrated here for *Argemone* (Fig. 7) and *Dicentra* (Fig. 6), etc., is notable. Although a number of instances may be found in families of Ranunculales, other examples (*Valeriana*, *Isomeris*) are from unrelated families. The occurrences in Ranunculales are significant because one can seek correlations for those examples in which the median radial patterns are most prominent. The median radial bands of vessels are least prominent in Ranunculales that are arboreal (*Euptelea* Siebold & Zucc.), shrubby with a single basal stem (*Berberis* L., *Decaisnea* Hook.f. & Thomson), or lianoid (various Lardizabalaceae and Menispermaceae). The median radial configuration of vessel distribution is most prominent in plants with canelike stems (*Isomeris*, *Nandina* Thunb., *Valeriana*) or subshrubs that branch frequently near the base (*Argemone*, *Dicentra*, *Xanthorrhiza*) (Carlquist 1995a,b). The term "canelike" here connotes dicot stems that tend to branch from the base of a plant, stems that have limited accumulations of secondary xylem, increments of which tend to decrease during the several years of the life of a canelike stem.

One important feature of the species cited as having median radial vessel bands is that they all have wide multiseriate rays. This seems a clue to the probable significance of this pattern. The sum of anatomical features and habitat characteristics of the species with these median radial vessel bands suggests that both conductive safety and mechanical strength are involved. The advantages of contacts among vessels in radial groupings have been detailed above. The layers of fibrous cells between the vessels and the rays potentially protect the water columns of the vessels from shear and offer maximal mechanical strength (especially at stem bases) to the relatively slender stems of dicot species with canes. The wide multiseriate rays presumably provide flexibility. The paucity or absence of contacts between vessels and rays in the species with median radial vessel bands does not seem to be related to any disadvantage of contact between a vessel and a ray cell. Rather, the mechanical value of sheets of fibers uninterrupted by vessels seems the most important factor in this type of non-random vessel distribution.

Cable Construction by Sheathing of Vessels: a Liana Strategy

One might imagine, as did Müller in 1866 (cited in Haberlandt 1914: 690–696) that one or a few vessels encased in a fibrous cylinder that is embedded in thin-walled parenchyma would offer an ideal template for a cable construction unit: strength plus flexibility, protection of a conductively efficient conduit. Such a template is realized, in fact, in a number of lianoid dicots (e.g., species of *Antigonon* Endl., *Ipomoea*, and *Thunbergia*). There are many dicots, however, that have versions of cable construction different from that ideal template. *Clematis* has wide rays and shows various placements of fiber bands and thus is transitional between median band vessel groupings and vessels isolated within cylinders of fibers. *Clematis* might be expected to have some genetic basis for this pattern, since it is in the same family as *Xanthorrhiza*, Ranunculaceae, a family close to Papaveraceae. However, the construction of canelike stems and lianoid stems may not be very different physiologically and mechanically in dicots. Resistance to shear and torsion characterize both, and both have limited accumulations of secondary xylem. Canelike stems tend to have a higher proportion of vessels to fibers than lianas, judging from the species surveyed for this study.

Perhaps the most common type of lianoid structure features wedgelike fascicular areas of vessels embedded in fibrous tissue, areas separated from each other by wide rays. This is exemplified by such genera as *Aristolochia* L., *Polygonum* (vining species), and *Vitis*. *Clematis alpina* exemplifies this structure, with wide rays composed of notably thin-walled parenchyma cells. Lianoid patterns do not require thin-walled parenchyma in rays in order to achieve flexibility. A differential in strength, so that ray cells rather than fibers or vessels bend and absorb torsion, is to be expected, however.

Further progression in formation of cable structure in lianas is exemplified in the present study by *Cayratia* (Vitaceae) and *Coccinia* (Cucurbitaceae). These are larger lianas with wider diameter vessels. Axial parenchyma distribution is increased so that each such fibrous cylinder (most with a single large vessel each) is embedded within parenchymatous tissue.

Strands of fibers that enclose varying numbers of vessels and that are embedded in a parenchymatous background can also result from special types of meristematic action. Proliferation of axial parenchyma can result in splitting of fascicular areas, as in *Bauhinia* and some other woody lianas (Obaton 1960). In the present study, *Mendoncia* represents such activity. The genera *Bosea* L. of Amaranthaceae (Carlquist 2003a), *Anredera* Juss. of Basellaceae (Carlquist 1999) and, in Gnetales, *Gnetum* L. (Carlquist 1996) provide wonderful examples of the roles that successive cambia can play in providing parenchyma background tissue leading to a background for fibrous segments, thereby achieving cable construction.

The types of cable construction cited above in lianas show the importance of preserving the integrity of water columns in wide-diameter vessels (Putz 1983; Putz and Holbrook 1991; Rowe and Speck 1996). The presence of wide-diameter vessels has long been recognized as characteristic of vines and lianas (see Carlquist 1985a) as a device for achieving adequate conduction in stems with limited size compared to those of self-supporting woody plants. Ewers et al. (1991) show that in lianas, wide vessels account for only 14% of the conductive tissue, but perform 95% of the conduction. Cable construction is an ideal mechanism for protecting these vulnerable large conduits. The nature of fibrous sheathing of vessels and the parenchymatous background of lianoid stems has been less commonly stressed. One notes that vessels contact few if any axial parenchyma cells, and are usually separated from parenchyma by two or more layers of fibriform cells. This condition obviously represents non-randomness in vessel distribution. These fibriform cells may be libriform fibers, although tracheids, which can offer a conductive system with great conductive safety that can supplement vessels, are present in a surprisingly large number of lianas. The presence of wide, non-subdivided rays, multiple xylem centers (e.g., *Serjania* Vell.) or plates of other tissue (e.g., the secondary phloem in stems of Bignoniaceae) has been cited earlier under the rubric “anomalous secondary thickening” by various authors (e.g., Metcalfe and Chalk 1950).

Vessel Patchiness: a Lianoid Strategy

The term “vessel patchiness” is applied here to a pattern in which vessels, although mostly solitary, occur in some sectors of the fascicular secondary xylem but not in others. The phenomenon occurs in certain Convolvulaceae, Icacinaceae, Loganiaceae (*Strychnos*) and Passifloraceae and is therefore defined by these occurrences. All of the species thus far identified with this phenomenon are lianoid and all have relatively narrow rays. Most importantly, the background of fascicular xylem in these species consists of tracheids and fibriform vessels.

One can say that in lianas there is relatively little lateral flow within the secondary xylem, as shown by the dye experiments of Ewers et al. (1991) and by the work of Fisher and Ewers (1992). Thus, sap flow in lianas as a whole may occur in a rather sectorial fashion whether or not vessel patchiness occurs.

In the lianoid species with patchy vessel distribution, conductive safety is theoretically potentially very high when the background consists of narrow vessels and tracheids, but

this circumstance does not fully explain the occurrence of vessel patchiness in all examples. Studies of three-dimensional flow patterns in these species are very much needed to explain this little-noted phenomenon.

Non-Randomness of Vessel Distribution in Relation to Stem Succulence

The example of *Misodendrum* has been included because it has latewood fiber strands but is not a lianoid plant. As a parasite on *Nothofagus* Blume, *Misodendrum* is a small shrub. Concentric arrangement of the fiber strands in latewood and the abundance of parenchyma elsewhere in the secondary xylem seem related to expansion and contraction of stem tissues. Certainly a stem parasite is likely to be subject to strong fluctuations in xylem pressures.

One can ask why *Misodendrum gayanum* and *M. punctulatum* seemingly lack such fiber strands. In fact, they do not: the (potential) ray areas (these species are rayless) and the fascicular areas except for vessels and axial parenchyma consist of fibers (plus vessels). These two species constitute *Misodendrum* subgen. *Misodendrum* sect. *Misodendrum* and the rayless wood condition is probably a recent synapomorphy if one places them on the tree offered by Vidal-Russell and Nickrent (2007). Thus, these two species may represent a recent shift to a strength-based system rather than an expansion-contraction-based system for dealing with negative pressures in xylem.

Succulents with a single cambium rarely show concentric rings of vessel-bearing parenchyma in secondary xylem. Such rings, alternating with strands of fibers free from vessels, do occur in *Portulacaria* Jacq. (Carlquist 1998). Radial expansion (by means of radial cell elongation) occurs in concentric zones of vessel-free parenchyma in stems of some species of *Fouquieria* Kunth., notably *F. columnaris* Kellogg (Carlquist 2001b). Some Cactaceae have expansion of parenchymatous vessel-free zones as a means of achieving wide parenchyma bands (Stone-Palmquist and Mauseth 2002). Most Cactaceae, however, have other mechanisms for achieving stem enlargement.

Growth Rings: Non-Randomness for Safety

There are significant changes in vessel grouping within some growth rings, and this variable needs to be considered. Earlywood tends to have smaller numbers of vessels per group than latewood. Exceptions are found, as might be expected, where vascentric tracheids are abundantly present (*Quercus*, etc.) and thus provide a form of safety evidently superior to that offered by vessel grouping.

Less well known is the absence or scarcity of vessels in latewood as a safety mechanism, as in *Ephedra*, Myricaceae, Rosaceae, globular cacti, etc. Thus tracheid presence trumps vessel grouping as a safety mechanism. In woods that have libriform fibers or fiber-tracheids as the background cell type, vessel grouping is a prime safety mechanism (Carlquist 1984, 2002): experimental testing is desired.

Successive Cambia: Diverse Plans, Diverse Functions

Successive cambia have been poorly understood ontogenetically (and therefore terminologically), and this has hindered

visualization of the ways in which various histological plans of species with successive cambia function. These functional relationships are only beginning to be appreciated (Carlquist 2007a). The role of non-randomness in vessel distributions of these plans has received very little comment. By virtue of presence of bands or concentric rings of conjunctive tissue, vascular increments and the vessels they bear are spaced apart from each other more than they would be in a wood with a single vascular cambium. (Arguably, a dicot wood with radially unusually wide bands of axial parenchyma could also qualify as exemplifying this tendency and is worthy of consideration as another representation of spacing of vessels radially).

About half of the taxa with successive cambia are lianoid or have scandent tendencies (Carlquist 2001a). This fact suggests a predisposition toward cable construction by such lianas. The classic instances (e.g., *Antigonon*, *Bauhinia*, *Gnetum*, *Mendoncia*) feature initiation of relatively few vascular cambia, but extensive separation of vascular areas by means of axial parenchyma proliferation. Cable construction also occurs, however, in genera in which a master cambium gives rise to numerous successive vascular cambia. In these genera, a stem consists of vascular increments separated from each other radially by conjunctive tissue and tangentially by rays (*Agdestis* Moc. & Sessé ex DC., *Anredera*, *Bosea*, *Bougainvillea*, etc.). There is evidence that cable construction is effective in safeguarding the conductive system against damage due to torsion (Putz and Holbrook 1991).

Non-random spacing of vessels in species with successive cambia makes stems and roots pre-adapted for storage functions (*Beta*, *Mirabilis* L.). The apparent longevity of vascular increments as evidenced by continual production of secondary phloem and xylem (Carlquist 2007a,b) and the production of conjunctive tissue between the bands are apparently effective patterns for input and retrieval of photosynthates. In Aizoaceae, most species of which have successive cambia (Carlquist 2007b), water storage often accompanies photosynthate storage.

Conversion of a stem to a fibrous background (*Stayneria*) and the absence of vessels from outer vascular increments (*Aptenia*, *Mestoklema*) are instances of non-random vessel distribution in Aizoaceae. These genera show the kinds of evolutionary repatterning towards mechanical strength and flexibility that can be achieved within the framework of successive cambia.

Even more amazing is the range achieved within Nyctaginaceae (Carlquist 2004), from tuberous roots (*Boerhaavia* Mill., *Mirabilis*) to lianas (*Bougainvillea* Comm. ex Juss.) to full-sized trees (*Guapira*, *Heimerliodendron* Skottsb., *Neea* Ruiz & Pav., *Pisonia* L.). Successive cambia are thus repatterned in ways that include concentric bands of storage parenchyma, cable construction, and woodlike conjunctive tissue, respectively.

Wider Implications of Non-Random Vessel Patterning

Non-random vessel distribution is morphogenetically easily achieved. The simplicity of the triggering is shown by the changes in number of vessels per group within a growth ring, from solitary vessels in earlywood to grouped vessels in latewood. Shift to non-random vessel patterns has only one

potentially negative side effect: placing a vessel at a greater distance from a cell with physiological mechanisms dependent on water supply. The occurrence of a tracheid background tissue in a vessel-bearing wood renders contacts with vessels not directly relevant, because a tracheid system, if much less efficient at conduction than vessels, multiplies the contacts between a water-conducting system and other cell types enormously. Comparative studies show the strong likelihood that the safety of a tracheid background in a wood trumps the value of vessel grouping in promoting conductive safety (Carlquist 1984). An all-tracheid background can even be “reshaped” into cable construction by distribution of axial and ray parenchyma (e.g., *Gnetum*). This enhances vessel safety two ways: by providing (1) a fibrous sheath protecting wide vessels from mechanical damage, and (2) a subsidiary conductive system adjacent to each vessel.

In dicot woods with fiber-tracheids or libriform fibers as background cell types, there is an inevitable division of labor between a conductive and a mechanical system. Non-random vessel distribution in the form of vessel grouping then becomes a primary means of achieving conductive safety. Like vessel density, vessel diameter, and wood cell wall thickness, vessel grouping becomes a change for promoting vessel safety that can, in theory, be readily achieved by action of regulatory genes. Comparative studies suggest such action, but experimental studies are needed to demonstrate it directly.

On a more global scale, the concept of vascular bundles needs examination in terms other than descriptive. Aggregation of vessels (or tracheids) into vascular bundles or steles seems rarely questioned with respect to function. In functional terms, one might imagine that a more diffuse distribution of tracheary elements (separated from each other by parenchyma) within a root, stem, or leaf might serve to put tracheary elements in closer contact with more parenchyma cells, with fewer parenchyma cells therefore functioning in transferring water laterally. The possible function of vascular bundles in promoting strength and conferring safety to the conductive system is evident in monocots in which fibrous bundle sheaths occur: this is an example of cable construction. Cable construction, if not as dramatic in dicots or other groups of vascular plants, certainly is abundantly present in them.

The radial catenation of primary xylem tracheary elements is evident in primary xylem, but has received little comment. The radial arrangement of tracheary elements theoretically provides maintenance of conductive pathways, so that as a protoxylem tracheid is deactivated, a later-formed tracheid in contact with the deactivated tracheid remains functional. This continues, then, into metaxylem. Primary xylem is often in the form of radial plates of tracheary elements, separated by radial plates of parenchyma a single cell wide. The parenchyma theoretically provides an excellent tissue for accommodating expansion and contraction of primary xylem. This explanation is enhanced if one takes into account the commonness of parenchyma around tracheary elements around vessels in Crassulaceae (*Aeonium* Webb & Berthel., *Kalanchoe* Adans.) or globular cacti. Primary xylem in leaves consists mostly of elements with helical thickenings. In this case, the grouping of such tracheary elements together provides for simultaneous contraction and expansion with changes in water potential. By grouping of such tracheary elements, failure of any given tracheary element is probably lessened. Experimental studies

on individual cells in the context of a leaf are, of course, difficult, but comparative anatomy suggests that grouping of tracheary elements into bundles must be based on a positive functional value and is not random. Brodribb and Holbrook (1995) have shown that tracheids in leaf veins of the conifer *Podocarpus* Labill. deform under negative pressures but the tracheary cells ("transfusion cells" of some authors) adjacent to the tracheids fail. Cochard et al. (2004) have reported collapse of leaf tracheids of *Pinus* L. leaves under water stress. Certainly, simultaneity of contraction and expansion underlies the larger groupings of helically thickened tracheids that have been reported in globular cacti (Gibson 1973).

There is another type of non-random distribution of vessels that must be considered in physiological terms: the organographic distribution of vessels, as in monocots. For example, the roots of *Allium* L. have vessels with simple perforation plates, whereas stems and leaves of *Allium* have xylem that consists wholly of tracheids. This distribution seems related to the brevity of water availability to bulbs and the short longevity of their roots, compared to the persistence of stems and leaves in bulbs and their maintenance of water columns during dry seasons. Similar explanations have been offered with respect to monocotyledons with other vessel distributions and other ecological adaptations (Carlquist 1975: 106, 115). Few monocots have xylem in which vessels and tracheids exist side by side, although a few do (*Borya* Labill.: Carlquist et al. 2008). These are only a few of the anatomical configurations in which non-random vessel distribution needs to be discovered and described.

Comparative studies can form a pathway along which experimental studies can proceed. Regulatory genes are almost certainly involved in some way. Nilsson et al. (2008) and Farquharson (2008) have implicated lower auxin levels in relationship to transverse and axial dimensions of fibers and vessel elements and discuss the possibility of a connection between auxin levels and regulatory genes. Wood cell groupings, as well as cell dimensions, should be investigated in this context.

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APPENDIX 1

Collection data for wild and cultivated species illustrated and discussed in the article are indicated or can be retrieved from the papers referenced below.

- Acanthaceae (*Mendoncia* Vell. ex Vand., *Thunbergia* Retz.): Carlquist and Zona 1988b
- Aizoaceae (*Aptenia* N.E.Br., *Mestoklema* N.E.Br., *Stayneria* L.Bolus): Carlquist 2007b
- Brassicaceae including Capparaceae (*Isomeris arborea* Nutt.): Carlquist and Hoekman 1985 (cultivated at Rancho Santa Ana Botanic Garden, Claremont, CA)
- Cactaceae (*Mammillaria mystax* Mart.): cultivated in Santa Barbara, CA
- Convolvulaceae (*Breweria* R.Br., *Ipomoea* L., *Operculina* Silva Manso): Carlquist and Hanson 1991

- Cucurbitaceae (*Coccinia* Wight & Arn.): Carlquist 1992a
- Fagaceae (*Quercus* L.): Carlquist and Hoekman 1985
- Misodendraceae (*Misodendrum* Banks ex DC.): Carlquist 1985b
- Nyctaginaceae (*Guapira* Aubl.): Carlquist 2004
- Papaveraceae (*Argemone* Tourn. ex L.): Carlquist et al. 1994; (*Dicentra* Bernh.): Carlquist and Zona 1988a
- Polygonaceae (*Polygonum* L.): Carlquist 2003b
- Proteaceae (*Grevillea rosmarinifolia* A.Cunn.): cultivated in Santa Barbara, CA
- Ranunculaceae (*Clematis* L., *Xanthorrhiza* Marshall): Carlquist 1995c; (*Clematis haenkeana* C.Presl): SJRW-34198
- Rhamnaceae (*Ceanothus* L.): Carlquist and Hoekman 1985
- Valerianaceae (*Valeriana* L.): Carlquist 1983
- Vitaceae (*Cayratia* Juss. sp., NSWw-R-1229-12; *Vitis vinifera* L., cultivated in Claremont, CA)